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A preliminary report on carnivorous mammals from Pondaung fauna

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Abstract

Some carnivore materials have been discovered from the Pondaung Formation in central Myanmar recently. The materials are separable into at least two genera, both of which are hyaenodontid creodonts. One of them is a medium-sized proviverrine. Collected parts include a maxilla, lower molar fragments, and some postcranial fragments. It shows some distinctive dental characters such as small protocone lobe on P^4, anterolingually-placed protocone and posterolingually-placed metacone relative to paracone on M^1 and M^2, and relatively large M_3 with a very reduced metaconid. The other is a much larger form. A maxillary fragment with a M^1 and a mandibular fragment with P_2 to M_2 have been found for this form. It possesses some similarities to *Pterodon*, but observations on more complete specimens and comparisons with other *Pterodon*-like hyaenodontids from Asia are necessary to settle a systematic assignment of this form. The two hyaenodontids are the only known mammalian predators from Pondaung fauna (latest Middle Eocene) based on the current knowledge.

Since early in this century, many vertebrate fossils have been collected from the Pondaung Formation (latest Middle Eocene; central Myanmar). Mammals known from the Pondaung fauna belong to a variety of taxa: Artiodactyla, Creodonta, Perissodactyla, Primates, and Rodentia (Takai *et al.*, 1999). Based on the current knowledge, only the creodonts represented mammalian predators in the fauna. The existence of the order in the fauna had not been recognized until an fossil expedition was held in 1997. Except that a few photos of the specimens appeared in the expedition report (Pondaung Fossil Expedition Team, 1997), any information on these creodont fossils have never been published yet. This report intends to introduce carnivorous mammal materials discovered from the Pondaung Formation in the recent expeditions and to provide more detailed information on the specimens.

The materials included here were collected by the Pondaung paleontological research team in 1997, by Myanmar – U.S. joint paleontological team in 1997 and 1998, and by

Table 1. Measurements for Hyaenodontidae indet. A. All measurements in mm. Numbers in parentheses indicate that the measurement is an approximation. (a) Upper dentitions. All measurements were taken from NMMP-KU 0042. (b) Lower dentitions. Measurements of M_1, M_2, and M_3 were taken from NMMP-KU 0045, 0046, and 0043, respectively.

(a)

	C^1	P^3	P^4	M^1	M^2	M^3
height	24.6	-	10.9	-	-	-
length	15.1	(12.5)	12.3	11.9	15.7	8.9
width	9.4	(6.3)	8.5	10.4	15.5	(16.4)
metastylar length	-	-	-	5.5	7.7	-

(b)

	M_1	M_2	M_3
height	-	9.0	-
length	12.0	-	-
width	5.6	6.3	9.3
trigonid length	6.9	7.4	10.2
talonid length	5.7	-	-
talonid width	5.5	-	-

Myanmar–Japan joint paleontological team in 1998 and 1999. All materials are stored in National Museum of Myanmar. They are serially catalogued under NMMP-KU (National Museum of Myanmar, in Paleontology – Kyoto University) specimen numbers. Field numbers are also provided in the parentheses.

The materials mentioned here have been collected from six different fossil localities in Pondaung region of central Myanmar (Aung Naing Soe, 1999; Aung, 1999; Tsubamoto *et al.*, this volume). Observations made on the materials indicate that the carnivores were represented by at least two hyaenodontid creodont genera in Pondaung fauna. Descriptions on the dental materials are given in the following paragraphs.

Hyaenodontidae indet. A

Material — NMMP-KU 0042 (Kdw-1), maxilla with right and left canines, right P^4 – M^2, and left M^2, a mandibular fragment, dental fragments, cranial fragments including left and right jugal bones and occipital part, and skeletal parts including vertebrae, ribs, humeri, femoral head, and proximal tibia; NMMP-KU 0043 (Kdw-2), a left M_3 fragment; NMMP-KU 0044 (Kdw-4), upper left I^{2-3}; NMMP-KU 0045 (Bhn-31), a right mandibular fragment with M_1; NMMP-KU 0046, a right M_2 fragment; NMMP-KU 0214, dental fragments including talonid parts of right M_2 and right M_3; NMMP-KU 0301 (Kdw-3), a left lower canine; NMMP-KU 0302 (Kdw-5), a right lower canine.

Locality — NMMP-KU 0042, 0043, 0044, 0301, and 0302 were collected from near Kyaw Daw Village, Palé Township; NMMP-KU 0045, 0046, and 0214 were collected from near Bahin area (site name Bh1), Myaing Township.

Comments — NMMP-KU 0042, 0043, 0044, 0301, and 0302 were collected from the same point and seem to belong to one individual; thus, these five specimens should be catalogued under a same specimen number. A proximal part of left IVth metatarsal (NMMP-KU 0256) was collected from near Pakkaung Village (site name Pk2), Bahin area, Myaing

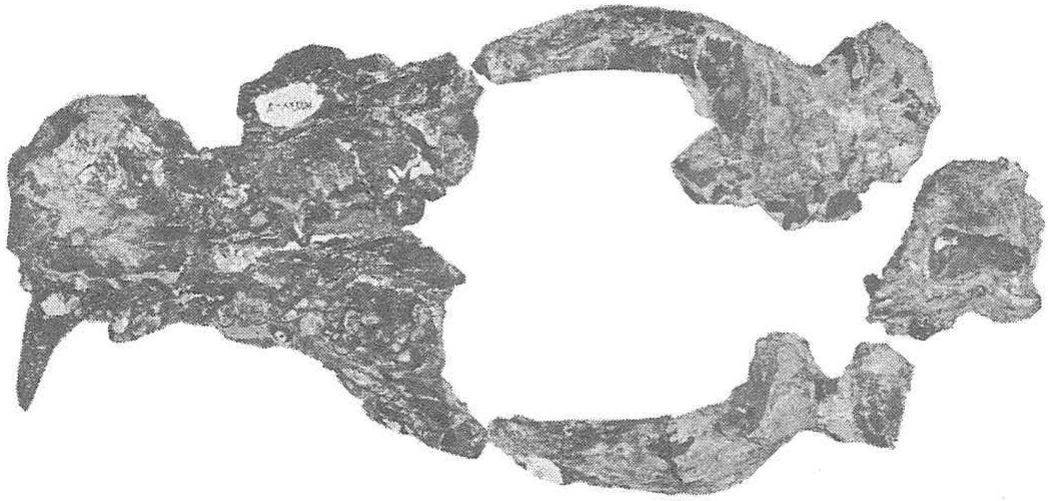

Figure 1. Skull of Hyaenodontidae indet. A in ventral view (NMMP-KU 0042). Skull length is estimated about 27 centimeters.

Figure 2. Right P^4-M^2 of Hyaenodontidae indet. A (NMMP-KU 0042): a) labial view and b) occlusal view. scale = 1cm.

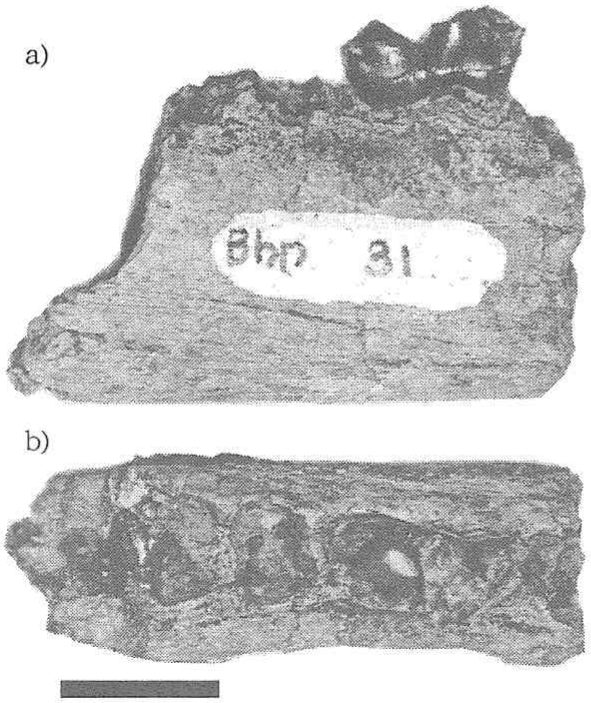

Figure 3. Right M_1 of Hyaenodontidae indet. A (NMMP-KU 0045): a) labial view and b) occlusal view. scale = 1cm.

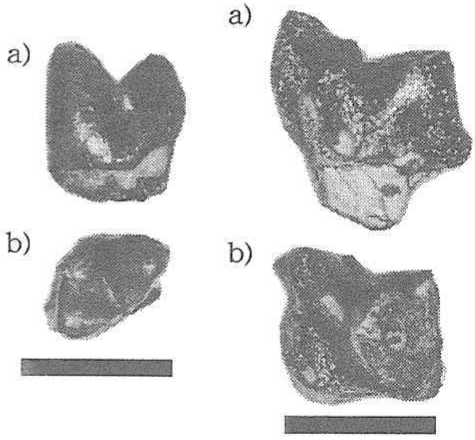

Figure 4 (left) . Right M_2 trigonid of Hyaenodontidae indet. A (NMMP-KU 0046): a) labial view and b) occlusal view. scale = 1cm.

Figure 5 (right). Left M_3 trigonid of Hyaenodontidae indet. A (NMMP-KU 0042): a) labial view and b) occlusal view. scale = 1cm.

Township. Based on the size, this specimen may also belong to this species.

Description on dental material — This species is a medium-sized hyaenodontid (Figures 1 - 5). Teeth have smooth enamel structure, except that crenulations are observed on the enamel of canines.

In upper incisors, I^3 is clearly larger than I^2. Upper premolars except P^4 are double-rooted. P^4 has three roots. Protocone lobe (internal swelling) is present only on P^4. It is small and lacks protocone. Relative to M^1, M^2 and M^3 are about 130% and 75% in length (Figure 2). On M^1 and M^2, the paracone and metacone are confluent: i.e., they are not fused, but closely attached. The two cusps are about equal in size and height, and conically-shaped. The metacone locates posterolingually to the paracone. The protocone is smaller than the other two cusps, but well-developed. The position of the protocone is anterolingual to the paracone. Weakly-developed cingulum surrounds the protocone. Stylar shelves are very narrow, and ectoflexes can not be well-defined. Metastylar blade is medium-sized, and transversely oriented. Postmetacrista is prominent. The postmetacrista and metastylar blade is discontinuous due to presence of carnassial notch. Only on M^2, small parastyle and paraconule are present, and a ridge from the parastyle connects to preparaconule crista. Shape of M^3 is labiolingually-elongated triangular.

Table 2. Measurements for Hyaenodontidae indet. B. All measurements in mm. Numbers in parentheses indicate that the measurement is an approximation. (a) Upper dentitions. All measurements were taken from NMMP-KU 0304. (b) Lower dentitions. Measurements were taken from NMMP-KU 0261 and 0262.

(a)

	P^3	P^4	M^1
length	(20.1)	(23.6)	-
width	(11.5)	(16.7)	(17.4)

(b)

	P_2	P_3	M_1	M_2	M_3
height	9.8	12.0	17.8	-	19.0
length	15.1	18.1	22.2	(17.9)	-
width	(8.7)	10.5	13.1	8.5	12.1
trigonid length	-	-	-	11.0	16.1
talonid length	-	-	-	5.1	-
talonid width	-	-	-	8.4	-

Paracone is larger than metacone, and the two cusps are almost fused except at the apeces. Protocone is not as high as the other two cusps. Parastyle is present, and the parastylar blade connects to the paracone.

Mandible is thick, and the height measures 18.8 mm at the bottom of M_1. Among lower molars (Figures 3 - 5), size of trigonid greatly increases from M_1 to M_3. Paraconid is smaller than protoconid, and sits anterolabially to the protoconid. Metaconid is smaller than protoconid and paraconid. Relative sizes of the cusp to protoconid decrease from M_1 to M_3, and metaconid is very small on M_3. The metaconid is placed posterolabial to the protoconid on M_1 and anterolabial to the paraconid on M_2 and M_3; thus, the trigonid is open in M_1 and closed in M_2 and M_3. Talonids on lower molars are basined, and have distinct hypoconulid and entoconid. On M_1, talonid is round and unreduced (talonid length to trigonid is about 80%). M_2 talonid is about equal to M_1 talonid, and M_3 talonid is smaller than M_1 and M_2 talonids in absolute size. On M_3, talonid is greatly reduced relative to trigonid, and shape of the talonid is narrow.

Hyaenodontidae indet. B

Material — NMMP-KU 0261, a right mandibular fragment with P_{2-4}, and talonid of M_1; NMMP-KU 0262, right M_1 and M_2 (anterior cuspids); NMMP-KU 0304 (mgg-1), a left maxillary fragment with M_1.

Locality — NMMP-KU 0261 and 0262 were collected from about 2 km north from Thadut Village, Bahin area, Myaing Township. NMMP-KU 0304 was collected from near Mogaung Village, Palé Township.

Comments — NMMP-KU 0262 consists of fragments broken from NMMP-KU 0261, and these two specimens should be catalogued under a same specimen number.

Description on dental material — This second hyaenodontid species is clearly larger

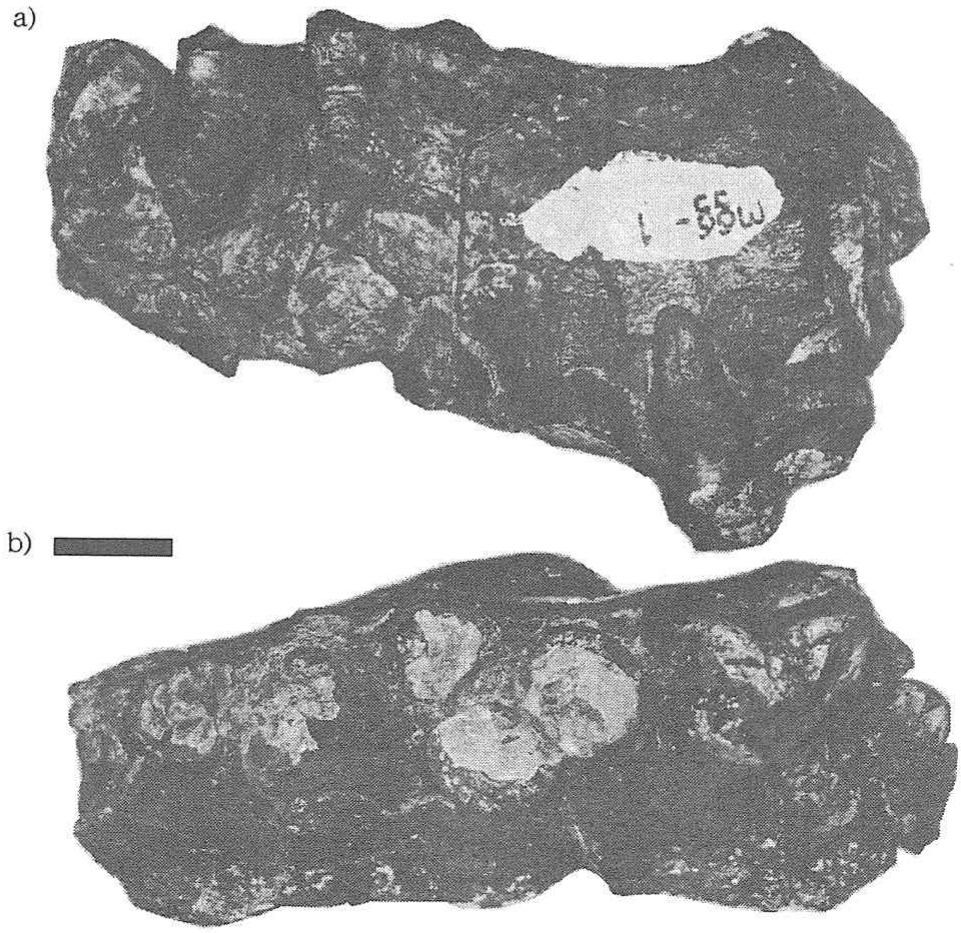

Figure 6. Left maxillary fragment with M^1 of Hyaenodontidae indet. B (NMMP-KU 0304) : a) labial view and b) occlusal view. scale = 1cm.

than the first form (Figures 6 and 7). Teeth are more robust and massive, and dental surface indicates a crenulated enamel structure.

On the maxillary fragment (Figure 6), crown part of the teeth was preserved only for M^1. The base part remains for P^4, and the shape indicates that the tooth had a large protocone lobe. P^3 may also havea small protocone lobe based on the shape of the base. On M^1, paracone and metacone are fused to one another. The shape of metacone is conical, and the cusp sits posterolingual to the paracone. Basal diameter is larger in paracone than in metacone. The tip of the cusps are broken, but the heights look about the same. Protocone has very low height and positions anterolingually to the paracone. There is a small paraconule. Ectoflexus is shallow, and very narrow stylar shelf separates paracone and metacone from labial margin of the crown. Parastyler blade is short, and does not connect with preparaconule crista but with the paracone. Postmetaconule crista is obscure. There

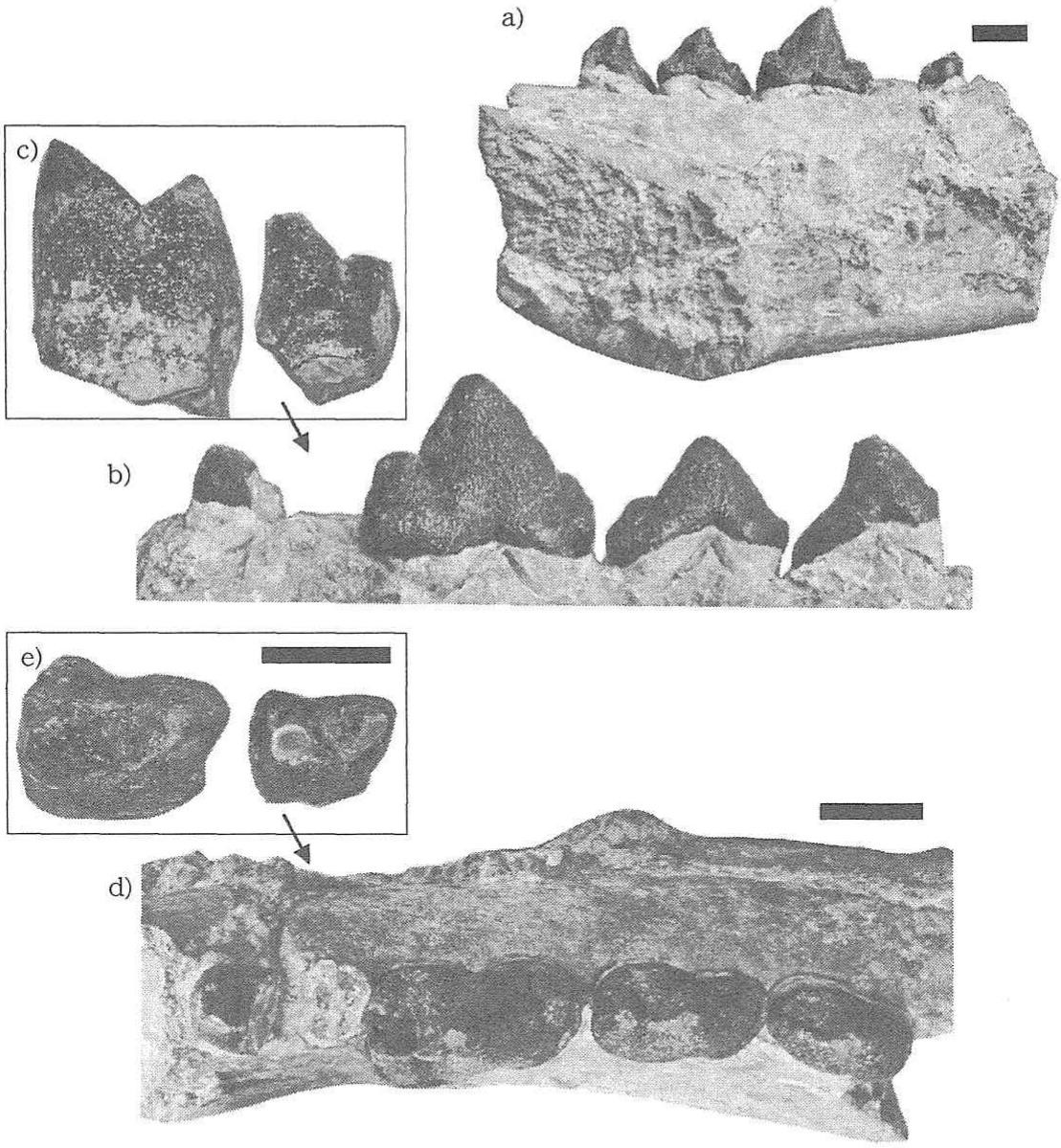

Figure 7. Right mandibular fragment with P_2-M_2 of Hyaenodontidae indet. B (NMMP-KU 0261 and 0262): a) lingual view of the mandibular fragment, b) labial view of P_{2-4} and base of M_1, c) labial view of M_1 and M_2 trigonids, d) occlusal view of P_{2-4} and base of M_1, e) occlusal view of M_1 and M_2 trigonids. scale = 1cm.

is no obvious carnassial notch, and the crista is continuous with metastylar blade. Because the posterior part of M^1 is not preserved, length and orientation of the metastylar blade are unknown.

Mandible is robust (Figure 7). The height of the mandible is 43.3 mm below M_1. The mandibular symphysis extends posteriorly to below P_3. Tooth rows from P_2 to M_1 are closely packed. P_1 is absent or very small, since there is not much space between root facets for canine and P_2. P_2 lacks any accessory cusps. P_3 is larger than P_2 in length, and the two premolars are about equal in height. P_3 has a small posterior accessory cusp on the

postprotocristid. P_4 is larger than P_2 and P_3, as well as than M_1. On P_4, a small anterior accessory cusp locates anterolingually to the main cusp. The posterior accessory cusp of P_4 is better developed than that of P_3. It connects to the entocristid, and a basined talonid is present. On the all premolars, weakly-developed cingulum surrounds the crown. On M_1 and M_2, the metaconids are vestigial. The paraconid locates anteriorly to the protoconid, and the latter cusp is larger. On the M_1, talonid is round and basined. It is slightly reduced relative to the trigonid, and the length of talonid to trigonid is about 46%. The shape of the trigonid on M_2 is very similar to that on M_1, but the trigonid of M_2 is about one and a half times larger than that of M_1. The talonid of M_2 are not preserved.

Other carnivorous mammal material

In addition to the above mentioned materials, NMMP-KU 0303 (Tudw-1) was collected from Than U Daw Village, Myaing Township. This specimen is a left mandibular fragment with a fragment of M_3. The inferior part of the mandible is broken, and its precise height is unknown. It is about the size of Hyaenodontidae indet. A; however, the mandibular corpus of NMMP-KU 0303 looks much more gracile than that of the Hyaenodontidae indet. A (NMMP-KU 0045). The cusps are very poorly preserved, but the shape of base of the M_3 indicates that it had an unreduced talonid. This specimen most likely belonged to an carnivorous mammal, Creodonta or Carnivora, but it can not be assigned to any families or genera because of its poor preservation condition.

Comments on systematic assignments for the Pondaung hyaenodontids

Hyaenodontidae is a highly diversified family, and 56 genera were recognized (McKenna and Bell, 1997). The fossil record of hyaenodontid creodonts begins in the Lower Eocene of North America and Europe; they spread to Asia and Africa before they became extinct in the Miocene (McKenna and Bell, 1997). The systematics within the family has not been well-solved, although some revisional studies to clarify the relationships among some members of the family have been published (e.g., Lange-Badré, 1979; Barry, 1988; Gingerich and Deutsch, 1989; Polly, 1996). The family has been divided into several groups, usually at the subfamily level. The included taxa and usage of ranks for the groups differ among the researchers, and this can cause great confusions. In this study, the systematic framework provided by Polly (1993, 1996) are used.

Among the subfamilies, Proviverrinae Schlosser, 1886, (≈ Proviverini *sensu* McKenna and Bell, 1997) is considered as a paraphyletic stem group, and it includes many primitive hyaenodontids as well as many derived later forms. Limnocyoninae Wortman, 1901, (≈ Limnocyonini *sensu* McKenna and Bell, 1997, and Limnocyonidae *sensu* Gunnell, 1998) is characterized by loss of third molars and relatively short skull length, and members of

this subfamily are limited in early to middle Eocene North America, except that two Chinese forms and one European form have been dubiously assigned to the subfamily. Hyaenodontinae Leidy, 1869, (≈ Hyaenodontini *sensu* McKenna and Bell, 1997; ≠ Hyaenodontinae *sensu* McKenna and Bell, 1997) includes several later hyaenodontid genera. Although the subfamily name has been widely used for hyaenodontids which have larger body size and more specialized carnassial teeth, monophyly of the group has been rejected by some recent studies (e.g., Polly, 1996), and some genera were removed to other subfamilies such as Hyaenailourinae Pilgrim, 1932, and Pterodontinae Polly, 1996. Apterodontinae Szalay, 1967, (= Apterodontini *sensu* McKenna and Bell, 1997) is another subfamily which is usually recognized in the family, and consists of only one genus, *Apterodon*, from the late Eocene to early Oligocene Egypt and the Oligocene Europe. Other genus, such as *Teratodon* and *Koholia*, have been included in Hyaenodontidae in some classifications, and placed in their own subfamilies (e.g., Teratodotinae *sensu* Morlo and Habersetzer, 1999, and Koholinae *sensu* Polly, 1993).

The first form of hyaenodontids from Pondaung fauna (Hyaenodontidae indet. A) lacks any diagnostic dental morphologies for the derived hyaenodontid subfamilies (e.g., loss of third molars, loss of metaconids on lower molars), and it should be placed in the subfamily Proviverrinae. As mentioned above, Proviverrinae is a paraphyletic stem group of Hyaenodontidae and includes many genera. Compared with early Eocene hyaenodontids, the first form of Pondaung hyaenodontids indicates rather derived conditions in some characters, such as partially appressed paracone - metacone and much smaller metaconids.

So far, the first form of Pondaung hyaenodontids looks most similar to *Paratritemnodon indicus* from early to middle Eocene of India and Pakistan, the northwestern part of Indian subcontinent. The similarities are found in the absence of protocone lobe on P^3, general shape of upper molars and lower molar trigonids, and relative size among lower molar trigonids (a description of *Paratritemnodon* was published in Kumar, 1992). However, there are some differences between the first form of Pondaung hyaenodontids and *Paratritemnodon*. These include absence of protocone on P^4 in the former, and smaller protocones on M^1 and M^2, greater degree of reduction of metaconid and relatively larger protocone on M_3, and larger body size in the former than in the latter. Because of these distinctions, the first form of Pondaung hyaenodontids, Hyaenodontidae indet. A, should be placed in a new genus.

The second form of hyaenodontids (Hyaenodontidae indet. B) from Pondaung fauna indicates a much more derived condition than the first form in having vestible metaconid on lower molars. Conicaly-shaped protocone and metacone on M^1 and the presence of talonid on M_1 place it in the subfamily Pterodontinae (*sensu* Polly, 1996; Holroyd, 1999) rather than the subfamily Hyaenodontinae (*sensu* Polly, 1996). Holroyd (1999) listed

several other diagnostic characters for Pterodontinae, but presence/absence of these characters in the second form of Pondaung hyaenodontids can not be examined due to the incompleteness of the materials.

Pterodontine hyaenodontids have been found from many localities in various continents (McKenna and Bell, 1997). From Asia, four species of "*Pterodon*" have been reported: "*P.*" *rechetovi* from the late Early Eocene Kyrgyzstan and the Middle Eocene Mongolia and Inner Mongolia, "*P.*" *hyaenoides* from the Middle Eocene Mongolia and Inner Mongolia, "*P.*" *dakhoensis* from the Middle Eocene China, and "*P.*" *exploratus* from the Late Eocene Mongolia (Matthew and Granger, 1925; Chow, 1975; Li and Ting, 1983; Dashzeveg, 1985; Tong, 1989; Lavrov, 1996; Lavrov and Averianov, 1998). However, a recent systematic revision restricted the use of genus *Pterodon* to the type species, *P. dasyuroides* from Europe, and four species from Africa (Holroyd, 1999). This revision coinsidized with the suggestions that Asian *Pterodon* species, such as "*P.*" *hyaenoides*, has more similarities to *Hyaenodon* than to European and African *Pterodon* and that it should be placed in the subfamily Hyaenodontinae (Polly, 1993, 1996). Lavrov (1996) pointed out that many *Pterodon*-like hyaenodontids satisfies only the part of the generic diagnosis, and he removed "*P.*" *rechetovi* to a new genus, *Neoparapterodon*, in Hyaenodontinae.

Compared the second form of Pondaung hyaenodontids with European and African *Pterodon*, structure of P_2-M_2 looks very similar between the two, except that heights of P_2 and P_3 relative to P_4 are slightly lower and that anterior accessory cusp of P_4 is slightly larger in the Pondaung form. The upper dentition of the Pondaung form, which is badly preserved, differs from that of *P. dasyuroides* in having protocone lobe on P^4 and posterolingually-placed metacone relative to protocone on M^1. The size and shape of P_2-M_2 of the Pondaung form resemble very well to those of "*P.*" *dakhoensis*. "*P.*" *dakhoensis* is known only from lower dentitions, and discovery of other elements which are useful for systematic classification may be necessary to confirm the similarity between the two. *Neoparapterodon rechetovi* is known only from the upper dentitions and cranial fragments, and the Pondaung form differs from *Neoparapterodon* in having much larger size, anteroposteriorly larger protocone lobe on P^4, and less reduced protocone on M^1. Compared with M_1 and M_2 of the Pondaung form, those of "*P.*" *exploratus* is two-thirds small and have more widely-opened paraconid-protoconid angle, suggesting that these two are probably in different genera. The Pondaung form is also very different from "*P.*" *hyaenoides*, which has large protocone lobe on P^4, lacks definite protocones on upper molars, and has completely fused and mediolaterally narrow paracone-metacone on M^1 and M^2. Some elements which are important for classification (e.g., better preserved M^2 and M_3) have not been discovered for the second form of Pondaung hyaenodontids. Generic assignment

of Hyaenodontidae indet. B may not be settled until the shortage of the morphological information is solved.

Summary

In Pondaung fauna of the latest Middle Eocene of Myanmar, two hyaenodontid creodonts were present. One of them, introduced here as Hyaenodontidae indet. A, is a medium-sized proviverrine. This form seems to be a new taxa which is similar to *Paratritemnodon* from the Early to Middle Eocene of Indian subcontinent, and detailed descriptions, a list of diagnostic characters, and analysis on its systematic position among Hyaenodontidae should be provided in elsewhere in future. The other, Hyaenodontidae indet. B, is a large and more derived hyaenodontid. The incompleteness of the material for this form and the confusion on the relationships among *Pterodon*-like hyaenodontids from Asia makes the systematic assignment of Hyaenodontidae indet. B more difficult. Another mandibular fragment may have belonged to a medium-sized carnivorous mammal.

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